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Meteorological Factors Influencing the Timing and Magnitude of Bloom by the Noxious Dinoflagellate *Karenia mikimotoi* in Two Bays of the Bungo Channel, Japan

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Abstract

The summer blooms of *Karenia mikimotoi* have recently tremendously damaged aquaculture industries in the Bungo Channel, western Japan. We statistically extracted meteorological variables correlated with the magnitude and timing of the summer bloom in Uwajima Bay and Saiki Bay located in the eastern and western coasts of the channel using data for ~13 y until 2017. We conducted field investigations in 2017 to understand the water quality characteristics in both bays. Meteorological conditions were almost totally similar, but *K. mikimotoi* population dynamics were different to varying degrees from year to year between both bays. Bloom timing significantly correlated with air temperature in March and April in Uwajima Bay and Saiki Bay, respectively. Bloom magnitude negatively correlated with hours of bright sunshine for 10 days before the bloom peak in Uwajima Bay and positively with precipitation and negatively with wind speed 5-10 days before the bloom peak in Saiki Bay. Field investigations showed that water temperature and salinity were always higher in Uwajima Bay and that nutrient concentration fluctuations were different in both bays. The present study indicates a possibility that meteorological factors influence *K. mikimotoi* population dynamics by means of water quality and local physical processes in both bays.

Discipline: Fisheries
Additional key words: irradiance, nutrients, Seto Inland Sea, temperature, wind

Introduction

Harmful algal blooms (HABs) have been a threat to fisheries, especially aquaculture industries, for many years in coastal areas around the world. Although accompanied by the quality loss of fishes, risks such as the unit price reduction of fish, and loss of confidence with customers, precautionary approaches, such as restrictions on fish feeding and early shipment, are some practical and effective mitigation techniques (Anderson 1997, Kim 2006, Shirota 1989). The monitoring of HABs in relation to environmental conditions can streamline precautionary techniques (Anderson 1997). However, because multiple factors related to the waxing and waning of HAB coexist in each sea area (Glibert et al. 2010), it is not realistic to monitor all of them, considering its cost and manpower. Therefore, determining the damages caused by HABs is one of the first steps in understanding the developmental patterns of an organism causing HAB and narrowing down factors that largely contribute to the bloom dynamics in the field. Statistical analysis is one of the tools in narrowing down these factors, and there are numerous previous studies targeted at various HAB species and sea areas (e.g., Dela-Cruz et al. 2002, Figueiras & Pazos 1991, Finnis et al. 2017, Mikaelyan et al. 2014, Onitsuka et al. 2015, Rounsefell & Dragovich 1966, Yamamoto & Okai 1996).

The dinoflagellate *Karenia mikimotoi* (Miyake & Kominami ex Oda) Gert Hansen & Moestrup forms blooms that kill marine animals, such as fish and

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shellfish, in the various coastal waters of Europe, America, South Africa, Australia, and Asia (Brand et al. 2012, Li et al. 2019). In China and Japan, this dinoflagellate is responsible for most cases of HABs from 1978 to 2018 (Sakamoto et al. 2021). Studies for a long time have accumulated knowledge about the taxonomy, ecophysiology, and toxicity of this dinoflagellate (e.g., Brand et al. 2012, Gentien 1998, Li et al. 2019). However, orthodox precautionary approaches are needed to be conducted to mitigate damages by *K. mikimotoi* bloom in each field because no specific technique for perfectly avoiding fishery damages has been developed.

Recently, the harmful blooms of *K. mikimotoi* have frequently occurred at the coastal waters of western Japan (Aoki et al. 2017, Li et al. 2017, Sakamoto et al. 2021). Especially, the fishery damage of 2012 in the coastal waters of the Bungo Channel (Fig. 1), a major production area of cultured fishes, such as yellowtail, red seabream, and tuna, in Japan, was the largest during the last decade (> 1.5 billion JPY; Setonaikai Fisheries Management Office 2013). However, there have been few research manuscripts addressing the relationship between *K. mikimotoi* bloom and the environmental factors in the Bungo Channel. Uwajima Bay (Ehime Prefecture) and Saiki Bay (Oita Prefecture) are located in the eastern and western coasts of the channel on a similar latitude (Fig. 1) and suffered areas from *K. mikimotoi* blooms. In the present study, we arranged the data of *K. mikimotoi* cell density in Uwajima Bay and Saiki Bay provided by Ehime and Oita Prefectures, respectively, during the past ~15 y when frequent monitoring of HABs had been conducted and explored meteorological factors closely related to the magnitude and timing of the bloom using correlation analysis. Meteorological factors can basically affect the development of a phytoplankton bloom (Yamamoto & Okai 1996), and consecutive data of them have been accumulated for many years and are therefore available for statistical analysis (Onitsuka et al. 2015). Moreover, we conducted yearly field investigations during the summer to understand the characteristics of water quality in both bays.

Materials and methods

1. Data used for analysis

We used the data of *K. mikimotoi* cell densities from 2004 to 2017 in Uwajima Bay and from 2006 to 2017 in Saiki Bay for statistical analyses. The data of Uwajima Bay and Saiki Bay were obtained from irregular spatiotemporal field observations by Ehime Prefectural Fisheries and Experiment Station and Oita Prefectural Agriculture, Forestry and Fisheries Research Center, respectively. The 2011 data in Uwajima Bay was removed from the analysis because the investigational frequency was much lower compared with the other years. In principle, the observations were conducted during daytime at a frequency from weekly to daily from May to August. The seawater for the counting of *K. mikimotoi* cells was sampled at least from surface and/or a depth where chlorophyll fluorescence was at the maximum in the water column on each observatory day. Chlorophyll fluorescence was measured using multiparameter water quality sensors (AAQ-RINKO, JFE Advantech Co., Ltd., Hyogo, Japan). Directly after sampling, the cells of *K. mikimotoi* were counted on a Sedgewick Rafter Cell Counting under a light microscope (magnification: 40× to 200×; ECLIPSE 80i, Nikon Co., Tokyo, Japan).

Meteorological data, such as precipitation, daily averages of air temperature and wind speed, and hours of bright sunshine, at meteorological observatories in Uwajima City and Saiki City were obtained from the website of the Japan Meteorological Agency (http://www.data.kishou.go.jp/etrn/index.html) (Fig. 1).

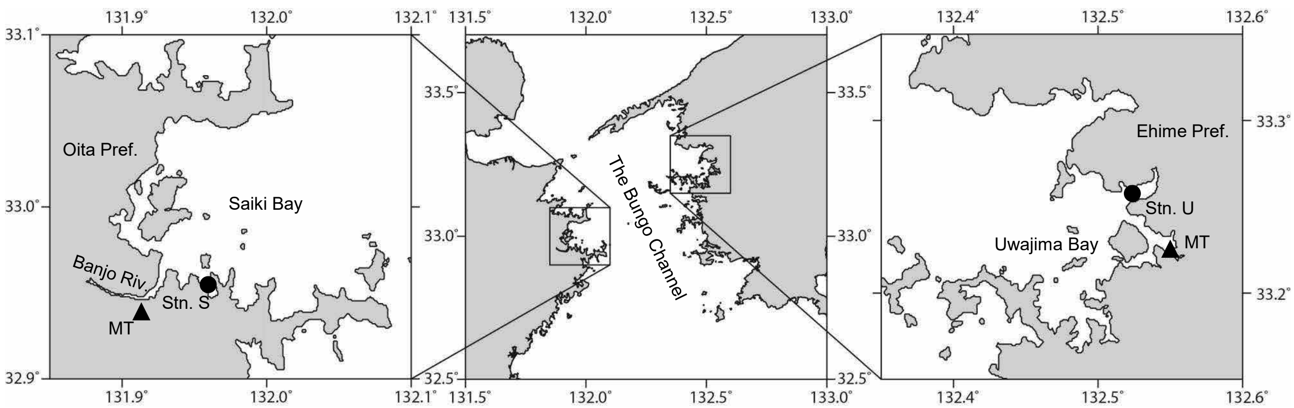

Fig. 1. Locations of meteorological observatories (MT) and investigatory stations in Uwajima Bay and Saiki Bay

2. Data analysis

We extracted days until first cell detection and until the bloom peak of *K. mikimotoi* as indicators of the timings of early growth phase and bloom occurrence and the maximum cell density and bloom duration of *K. mikimotoi* as indicators of bloom magnitude in each year. Days until first cell detection and days until the bloom peak were defined as the numbers of days from January 1 to the day when cell density first reached ≥ 1 cell mL^{-1} and the number of days from January 1 to the day when the maximum cell density was recorded, respectively, in each year. Bloom duration was defined as the number of days from the day when cell density first exceeded 100 cells mL^{-1} to the day when cell density of > 100 cells mL^{-1} was finally observed in each year. The bloom duration of 2007 could not be calculated because the cell density of *K. mikimotoi* was over 100 cells mL^{-1} at the first day of the investigation in Saiki Bay.

To explore the factors influencing the occurrence of *K. mikimotoi* bloom, we calculated the Spearman's rank correlation coefficients between meteorological variables and *K. mikimotoi* parameters, such as maximum cell density, bloom duration, and days until first cell detection and the bloom peak. Correlation analyses were performed under a level of statistical significance with P-value < 0.05 using IBM SPSS Statistics Desktop Version 19.0 for Windows (IBM Japan, Tokyo, Japan).

3. Investigations of water quality

To understand the characteristics of water quality in Uwajima Bay and Saiki Bay, we conducted field investigations from May to August in 2017. Stn. U and Stn. S, which were empirically recognized as the primary regions of *K. mikimotoi* bloom, were selected as investigatory stations (Fig. 1). Water temperature, salinity, and chlorophyll fluorescence were monthly measured at depths from 0 to 9 m using a multiparameter water quality sensor. Seawater for the analyses of nutrients, such as the dissolved inorganic nitrogen (i.e., the sum of nitrate, nitrite, and ammonium), dissolved inorganic phosphorus, and dissolved silicate, were sampled weekly from subsurface layers (Uwajima Bay: 3-m depth; Saiki Bay: 2- and 5-m depth), where *K. mikimotoi* cells accumulate during the daytime (Aoki et al. 2017, Shikata et al. 2017) using a Kitahara water sampling bottle (Rigosha & Co., Ltd, Saitama, Japan). Nutrient concentrations were determined using an AutoAnalyzer (SWAAT, BL TEC K.K., Osaka, Japan).

Results

1. Variations in the cell densities of *K. mikimotoi*

The timing and magnitude of *K. mikimotoi* were different to varying degrees from year to year between the two bays (Fig. 2), although meteorological conditions were almost entirely similar (data not shown). For example, in 2013, the maximum cell density in Saiki Bay was 1,855 times as high as that in Uwajima Bay. Days until first cell detection ranged from 130 (2014) to 185 days (2005) in Uwajima Bay and from 130 (2012) to 204 days (2006) in Saiki Bay. Days until the bloom peak ranged from 171 (2013) to 224 days (2017) in Uwajima Bay and from 154 (2016) to 233 days (2011) in Saiki Bay. In both bays, there were significant positive correlations between days until first cell detection and the bloom peak (Fig. 3), but these days had no significant correlations with the maximum cell density and bloom duration. The maximum cell densities of *K. mikimotoi* ranged from 11 (2013) to 310,000 cells mL^{-1} (2007) in Uwajima Bay and from 3 (2010) to 100,000 cells mL^{-1} (2007) in Saiki Bay (Fig. 2). Bloom duration ranged from 13 (2008) to 56 days (2017) in Uwajima Bay and from 21 (2016) to 68 days (2017) during years when maximum cell density exceeded 100 cells mL^{-1}. In both bays, there were significant positive correlations between the maximum cell density and bloom duration (Fig. 3), and the bloom durations were > 20 days during years when the maximum cell densities were > 10,000 cells mL^{-1}.

2. Meteorological variables selected using the correlation analysis

We calculated the correlation coefficients between days until first cell detection and until the bloom peak and monthly meteorological variables from January to May, the season before *K. mikimotoi* bloom, in each year (Fig. 4). However, because there were years when *K. mikimotoi* cells were detected in May, the meteorological data from January to April were applied to the correlation analysis with days until first cell detection. There was no significant correlation between days until first cell detection and meteorological variables in Uwajima Bay, but the air temperature in April negatively correlated with days until first cell detection and meteorological variables in Saiki Bay. There were significant negative correlations between days until the bloom peak and air temperature in March in Uwajima Bay and in April in Saiki Bay. Moreover, the wind speed in February positively correlated with days until the bloom peak in Uwajima Bay.

Moreover, we calculated the correlation coefficients between maximum cell density or bloom duration and the

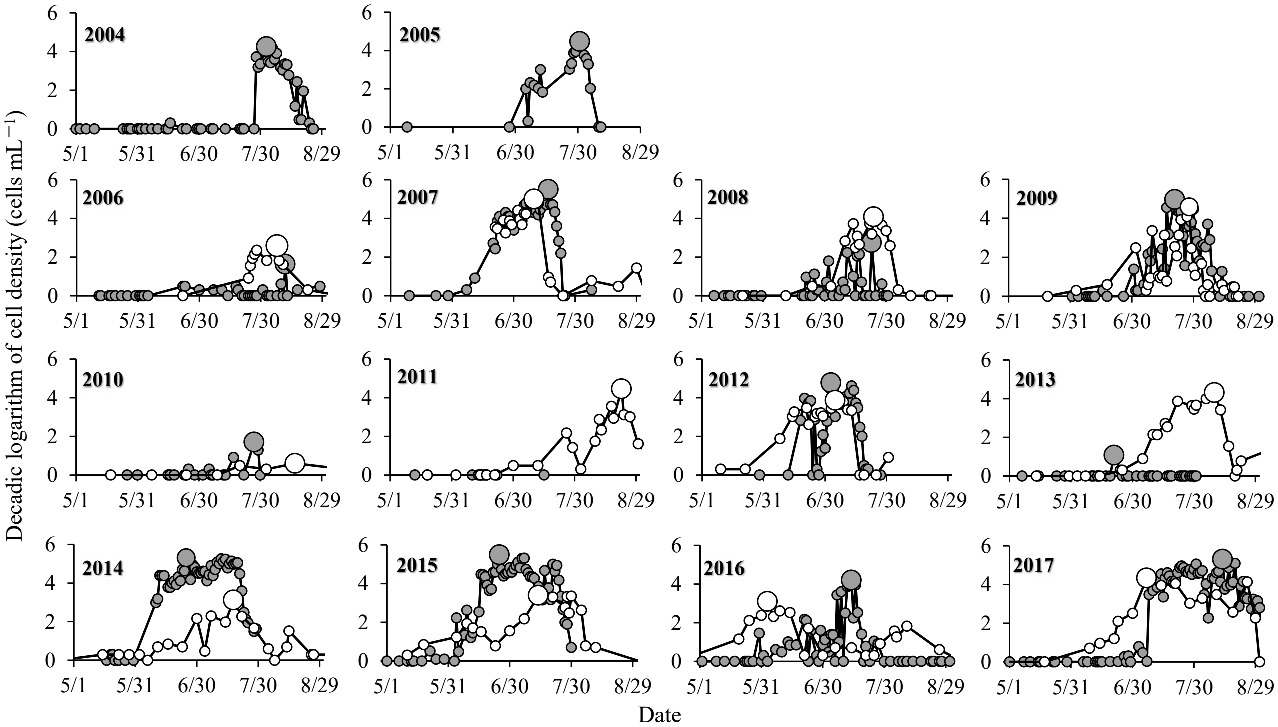

Fig. 2. Variations in the maximum cell density of *Karenia mikimotoi* in Uwajima Bay (gray circle) and Saiki Bay (white circle)

Larger plots represent maximum cell densities in each year.

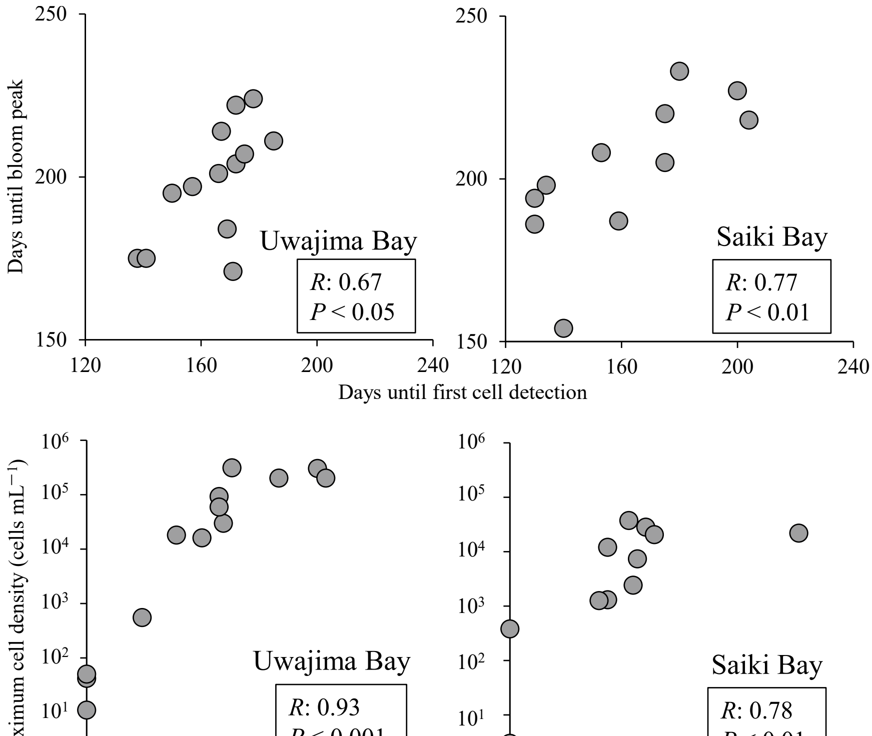

Fig. 3. Relationships between the indicators for the timing of bloom and between the indicators for the bloom magnitude in Uwajima Bay and Saiki Bay

Spearman's rank correlation coefficient (R) and P-value are also shown.

meteorological variables 5 (mean: 0-4 days), 10 (mean: 5-9 days), 20 (mean: 10-19 days), and 30 days (mean: 20-29 days) before and after the bloom peak in each year (Fig. 5). Precipitation positively correlated with maximum cell density and bloom duration 5 or 10 days before the bloom peak in both bays, but there were significant correlations only between precipitation and maximum cell density or bloom duration 5 days before the bloom peak in Saiki Bay. The correlation coefficient shifted to negative values in Saiki Bay 10-20 days after the bloom peak; however, it did not shift in Uwajima Bay. The absolute values of the correlation coefficient between air temperature and maximum cell density or bloom duration were low over the period in both bays. There were significant negative correlations between wind speed and maximum cell density 10 days after the bloom peak in Uwajima Bay and 5 days before the bloom peak in Saiki Bay. The correlation coefficient between hours of bright sunshine and maximum cell density or bloom duration increased to negative values 5 and 10 days before the bloom peak in Uwajima Bay and 5 days before and after the bloom peak in Saiki Bay. However, there were significant correlations only between hours of bright sunshine and maximum cell density or bloom duration 5 and 10 days before the bloom peak in Uwajima Bay.

3. Water quality

There were differences in water quality between Uwajima Bay and Saiki Bay, although the meteorological variables were always similar between the meteorological observatories of Uwajima and Saiki in 2017 (Fig. 6). The water temperature and salinity in Uwajima Bay were always higher than those in Saiki Bay. For nutrient concentrations, the levels were totally similar; however, the fluctuation patterns were different between the two bays. Variations in chlorophyll fluorescence were similar between the two bays.

Discussion

It has been reported that large blooms of *K. mikimotoi* persist for as long as 1-2 months in the waters of China, Japan, and some European countries (Aoki et al. 2017, Davidson et al. 2009, Qi et al. 2004). Similarly, the cell density of > 100 cells mL^{-1} were kept for > 20 days during the years with > 10,000 cells mL^{-1}, which is lethal for fish and shellfish (Helm et al. 1974, Matsuyama et al. 1998), in Uwajima Bay and Saiki Bay. Moreover, the maximum cell densities of *K. mikimotoi* exceeded 10,000 cells mL^{-1} nine times in 13 y in Uwajima Bay and six times in 12 y in Saiki Bay. These clearly show that massive blooms of *K. mikimotoi* have occurred frequently in the two bays recently.

First cell detection and the bloom peak were recorded from the beginning of May to the middle of July and from the beginning of June to the end of August, respectively, in both bays. These timings are roughly similar with those in the other sea areas of western Japan (Aoki et al. 2017, Honjo et al. 1991, Yamaguchi 1994). Similar to the previous study of Honjo et al. (1991), the present study confirmed the positive correlation between the timings of first cell detection and bloom peak. However, these timings had no significant correlation with bloom magnitude, as well as maximum cell density and bloom duration, indicating that different environmental factors may influence the timing and magnitude of *K. mikimotoi* blooms.

Previous studies indicate that most populations of *K. mikimotoi* spend all seasons as vegetative cells in warm embayments (Honjo et al. 1991, Itakura et al. 1990, Nakata & Iizuka 1987, Uchida et al. 1998); therefore, factors influencing the survival and growth of vegetative cells would regulate the population dynamics of *K. mikimotoi* in water columns. Recently, the cyst of this dinoflagellate was found in both laboratory and surface sediments (Liu et al. 2020). However, the encystment rate of artificially formed cysts is low (~10%), and the abundance of cysts in the field was very low; the excystment of cysts from the field was not observed. Moreover, the cyst is physically fragile due to its thin cell wall, and tolerance against adverse conditions, such as low temperature, has not been demonstrated. No report has demonstrated whether *K. mikimotoi* cysts were observed at the bottom sediments of Japanese waters where investigations using the Most Probable Number method have been frequently conducted (e.g., Imai & Itakura 1991, Shikata et al. 2008). Therefore, the growth of vegetative cells in water columns may contribute greatly to the initiation and development of *K. mikimotoi* at coastal areas in Japan in comparison with the germination of cysts.

Temperature is one of the main factors influencing the survival and growth of vegetative cells in *K. mikimotoi* (Yamaguchi & Honjo 1989); a culture strain of *K. mikimotoi* separated from western Japan can grow at ≥ 10°C, and the maximum growth rate is observed at 25°C. Honjo et al. (1991) suggested that the average water temperature from December to March negatively correlated with Julian days when the cell density of *K. mikimotoi* reached 1 cell mL^{-1} and 10^3 cells mL^{-1} in Gokasho Bay located 400 km-450 km east from Uwajima Bay and Saiki Bay. In Uwajima Bay and Saiki Bay, the air temperature before the bloom season also negatively correlated with days until bloom peak (Fig. 4). However, the significant correlation between air temperature and days until bloom peak was found only in March in Uwajima Bay and in April in Saiki Bay. The growth rate of *K. mikimotoi* rapidly increases at 15°C-25°C (Yamaguchi & Honjo 1989). The water temperatures around Uwajima Bay and Saiki Bay increase to 15°C-20°C from March to May, and the water temperature around Uwajima Bay has always been higher than that in Saiki Bay (Fig. 6; Suzuki & Takeuchi 2007, Yukihira 2013). These suggest that *K. mikimotoi* populations may temporarily become sensitive to temperature variations during the period of rising water temperature in both bays. Moreover, air temperature negatively correlated with days until first cell detection in Saiki Bay but not in Uwajima Bay (Fig. 4). The minimum water temperature around Uwajima Bay (~15°C) is higher than that in Saiki Bay (~13°C) according to previous long-term investigations (Suzuki & Takeuchi 2007, Yukihira 2013). Therefore, higher water temperatures may mitigate the effects of air temperature on the population dynamics of *K. mikimotoi* from winter to spring.

Conversely, the wind speed in February positively correlated with days until the bloom peak, whereas no meteorological variable correlated with days until first cell detection in Uwajima Bay (Fig. 4). There were cases in which the development of *K. mikimotoi* bloom followed nutrient concentrations after vertical mixing by wind blowing (Kimura et al. 1999), and Nakata & Iizuka (1987)

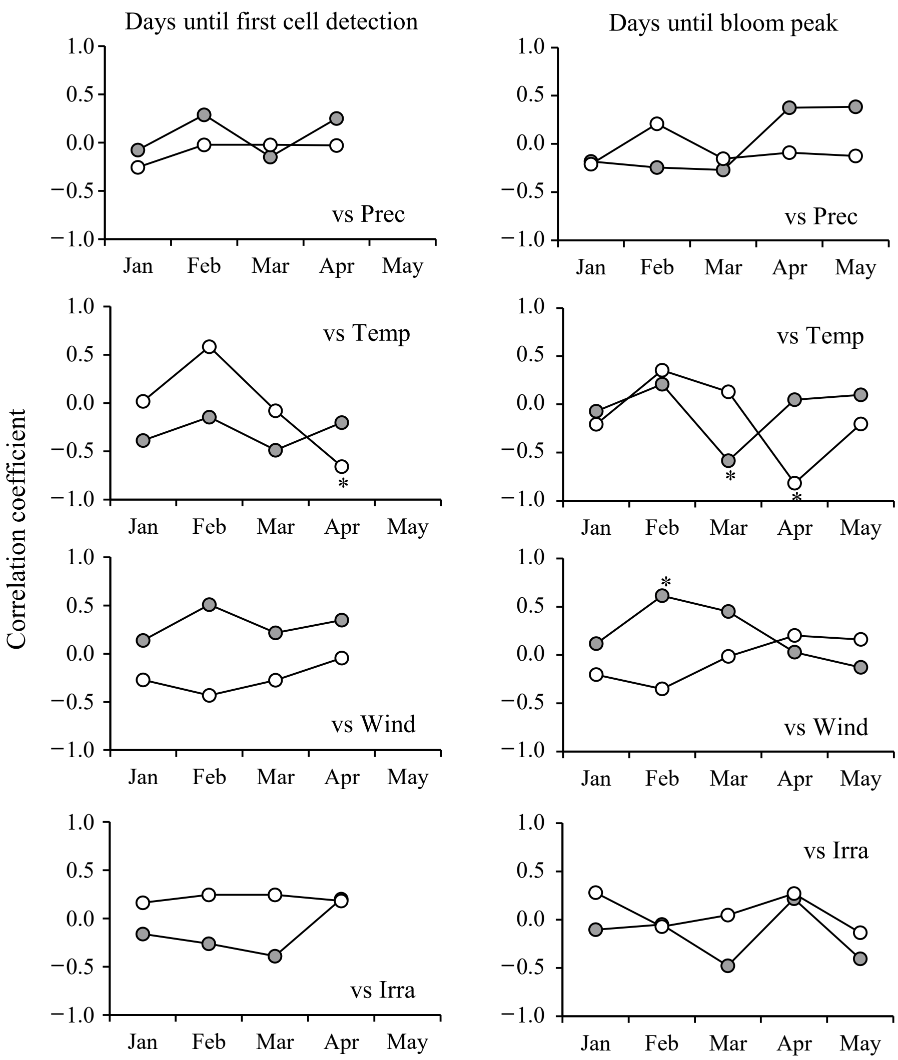

Fig. 4. Monthly variations in the Spearman's rank correlation coefficient timing of first detection and bloom peak and meteorological variables (precipitation: prec, air temperature: temp, average wind speed: wind, hours of bright sunshine: irra) in Uwajima Bay (gray circle) and Saiki Bay (white circle)
Asterisks represent correlation with significance ($P < 0.05$).

suggested that nutrient concentrations may affect the overwinter of motile cells and be responsible for establishing the next generation in spring in Omura Bay, western Japan, on the basis of field investigations and laboratory experiments. Wind direction can influence the development of *K. mikimotoi* bloom; the north wind tends to promote the occurrence of a bloom because the wind weakens the water exchange in Imari Bay, which is open to the north (Suzuki et al. 2008). According to the data of the Japan Meteorological Agency (http://www.data.kishou.go.jp/etrn/index.html), the western wind was predominant in Uwajima Bay, which is open to the west in February of most years. These indicate that wind may influence the maintenance of *K. mikimotoi* population from winter to early summer in Uwajima Bay.

Only meteorological variables within 10 days before and after the bloom peak of *K. mikimotoi* significantly correlated with the magnitude of bloom in the present study (Fig. 5). This corresponds to previous studies that demonstrated that the magnitude of bloom can be greatly influenced by environmental factors just before and after the bloom in *K. mikimotoi* (Barnes et al. 2015, Hartman et al. 2014, Kimura et al. 1999, Ouchi & Takayama 1984, Robin et al. 2013, Vandersea et al. 2020, Vanhoutte-Brunier et al. 2008).

Hours of bright sunshine within 10 days before the bloom peak negatively correlated with the magnitude of the bloom in Uwajima Bay and Saiki Bay, but there was a

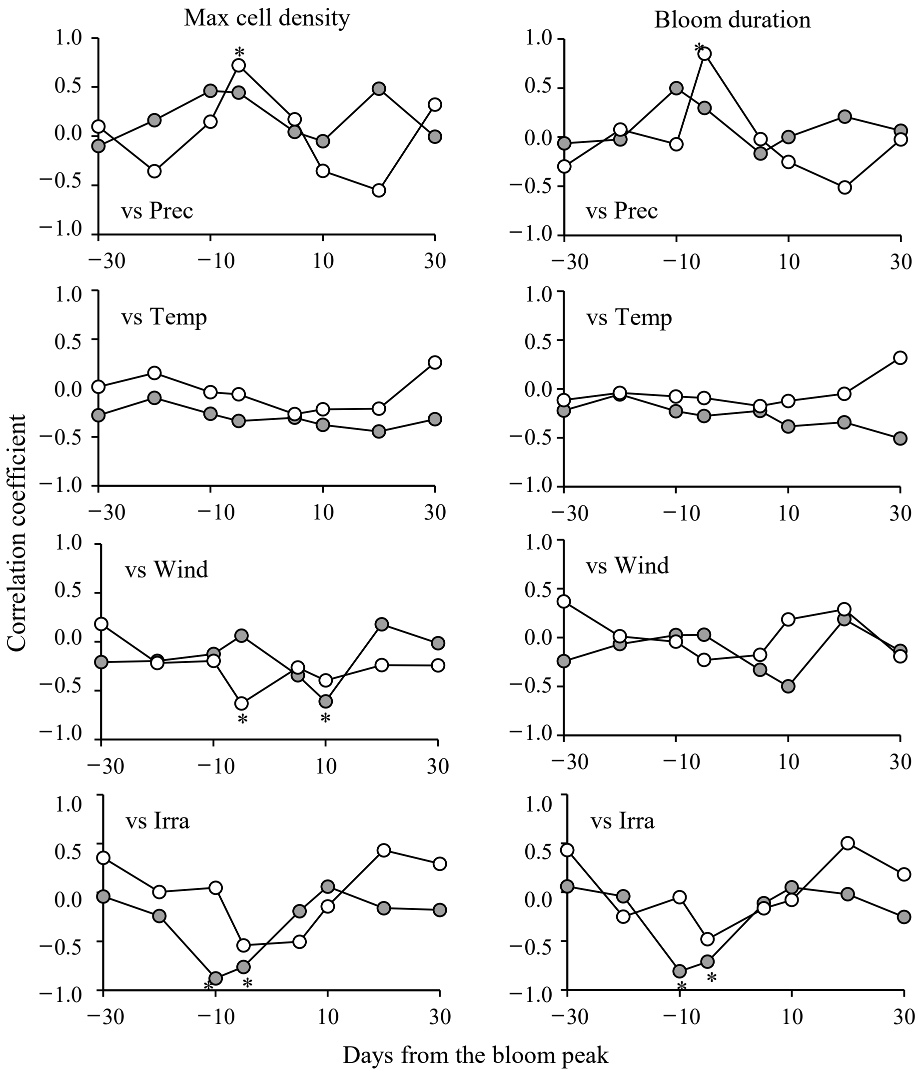

Fig. 5. Short-term variations in the Spearman's rank correlation coefficient between the bloom magnitude and meteorological variables (precipitation: prep, air temperature: temp, average wind speed: wind, hours of bright sunshine: irra) in Uwajima Bay (gray circle) and Saiki Bay (white circle)

Asterisks represent correlation with significance ($P < 0.05$).

significant relationship only in Uwajima Bay (Fig. 5). A previous report indicated that solar radiation before the massive bloom of *K. mikimotoi* was lower than the normal value in Iyo-Nada located ~35 km north from Uwajima Bay (Yanagi et al. 1992). The relationship between hours of bright sunshine and bloom magnitude in the field corresponds to the physiological characteristics of *K. mikimotoi*, i.e., cells can grow at low irradiance (Yamaguchi & Honjo 1989), and cells cannot survive under strong light in a nitrogen-deficient condition (Yuasa et al. 2018). The latter physiological property may be related to the differences in the correlation coefficient between Uwajima Bay and Saiki Bay because nutrient dynamics is greatly influenced by factors other than meteorological phenomena as will be described later.

Precipitation within 10 days before the bloom peak positively correlated with the magnitude of the bloom in both bays (Fig. 5). Massive *K. mikimotoi* blooms following precipitation and then flash from rivers have also been observed in other waters, such as Imari Bay, western Japan (Aoki et al. 2017), Scottish waters (Davidson et al. 2009), and English Channel (Hartman et al. 2014, Barnes et al. 2015). However, there were differences in the correlation coefficient between Uwajima Bay and Saiki Bay; the correlation was not significant in Uwajima Bay (Fig. 5). According to our investigation of water quality in 2017 (Fig. 6), in both bays, the concentrations of nitrogen and phosphorus are usually lower than the half-saturation concentration required for the growth of *K. mikimotoi* (nitrogen: 0.78 μM, phosphorus: 0.14 μM; Yamaguchi 1994), indicating that the growth of *K. mikimotoi* can be limited by nutrient concentration in both bays. However, the short-term fluctuations in nutrient concentrations are likely to differ between the two bays. It is known that nutrient dynamics are influenced by unique physical processes, such as *kyucho*, a sudden swift of current originating from a warm ocean current, the Kuroshio, in Uwajima Bay (Kawabata & Satake 1992, Takeoka & Yoshimura 1988). Water temperature and salinity were always higher during our investigation, indicating that the impacts from the open ocean on water quality may be stronger in Uwajima Bay than in Saiki Bay. Moreover, Uwajima Bay does not have a large river similar to the Banjo River of Saiki Bay (the largest river in the bay; Fig. 1), indicating that the impacts from the river on water quality may be weaker in Uwajima Bay than in Saiki Bay. The differences in the processes of supply and cycling of

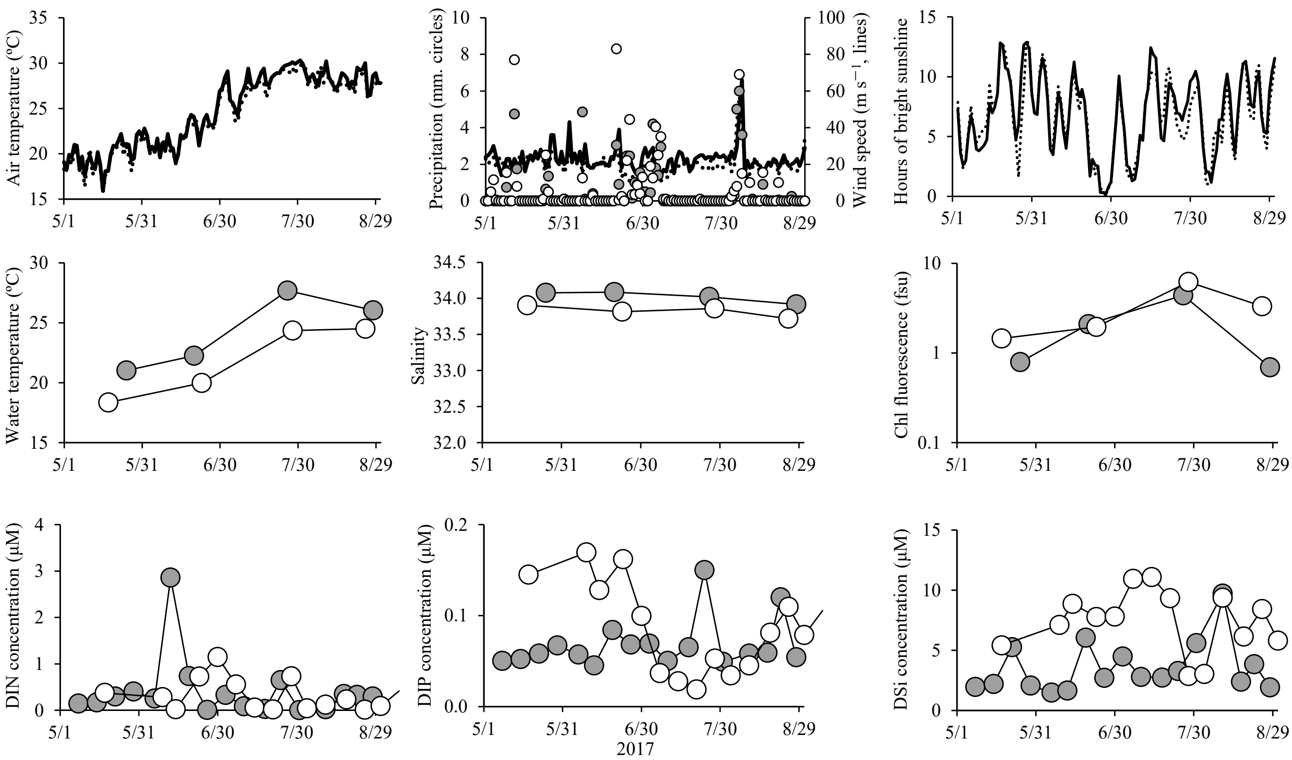

Fig. 6. Variations in meteorological factors and water quality at Stn. U (solid line, gray circle) and Stn. S (dashed line, white circle) in 2017

Hours of bright sunshine is the moving average for 3 days. Water temperature, salinity, and chlorophyll fluorescence are mean values from surface to 9-m depth. Nutrient concentrations are values at 3-m depth in Stn. U and at mean values of 2- and 5-m depth in Stn. S.

nutrients may influence the relationship between meteorological factors and *K. mikimotoi* population dynamics. To demonstrate this hypothesis, detailed field investigations, such as more frequent tracking of nutrient concentrations and quantitative analyses of physical processes, would be needed.

Wind speed 10 days before or after negatively correlated with maximum cell density in both bays (Fig. 5). However, according to the data of the Japan Meteorological Agency (http://www.data.kishou.go.jp/etrn/index.html), the wind direction in each period varied from year to year. The cells of *K. mikimotoi* swim to accumulate at surface or subsurface layers during the daytime (Koizumi et al. 1996, Shikata et al. 2017). Turbulence by wind can inhibit the cell accumulation of phytoplankton at upper layers (Seliger et al. 1970, Smayda 2002). In the two bays, oceanographic analysis is required to elucidate how wind influences the temporary dynamics of the bloom.

The present study presented some meteorological variables useful for understanding the current and near-future situations of the *K. mikimotoi* bloom in each bay of the Bungo Channel. The meteorological factors influencing the timing and magnitude of *K. mikimotoi* bloom are similar but correlate with period, and the correlation coefficients are different between the two bays. Moreover, the present study indicated that meteorological factors just before and after the bloom strongly influence the magnitude of the bloom and that the investigations of water quality and local physical processes can influence the relationship between bloom timing and magnitude. These suggest that the use of meteorological forecasting and the frequent investigations of water quality, such as nutrients, after the increase in cell density to some extent may help predict the bloom dynamics in the field.

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